

REGENERATION OF INJURIES AMONG JAMAICAN GORGONIANS: THE ROLES OF COLONY PHYSIOLOGY AND ENVIRONMENT

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ABSTRACT

The consequences of injury to reef dwelling colonial animals are determined partly by rates of regeneration of lost tissues. These experiments examined two potential influences on regeneration rates of Jamaican gorgonians: 1) intrinsic physiological and energetic differences among co-occurring, conspecific colonies differing in size, reproductive phase, or injury location; and 2) differential responses among three plexaurid species to changing environmental variables across their depth range. In *Plexaura homomalla*, regeneration rate varied with the location of injury within colonies, but was unexpectedly independent of either colony size or reproductive phase. In addition, colonies of *P. homomalla*, *Eunicea mammosa*, and *Plexaurella dichotoma* differed in relative ability to regenerate equivalent injuries in different reef zones across their depth range.

"There is one fact in the life-history of corals which the study of processes of repair clearly brings out, and it is this, that all the methods of regeneration are more for the life-saving of the colony than of the individual.

Wood-Jones, 1912

INTRODUCTION

Injury is common among arborescent Caribbean gorgonians during both catastrophic (e.g., hurricane) and routine conditions (Cary, 1914, 1918; Bayer, 1961; Kinzie, 1970, 1973, 1974; Birkeland 1974; Birkeland and Gregory, 1975; Kitting, 1975; Wahle, 1980; Woodley *et al.*, 1981). Moreover, injuries to Jamaican gorgonians can exhibit complex variation in both frequency and pattern among colonies living in different reef zones (Woodley *et al.*, 1981; Wahle, in prep.). Although many injuries are limited initially to a few cm of tissue (Cary, 1914; Kinzie, 1970, 1974), their effects on colonies can be subtle, delayed, and extensive. They can range from proportional reduction in the number of feeding, reproductive, and defensive polyps (e.g., Jackson, 1977, 1979), to disruption of colony-wide physiological integration (Bayer, 1961, 1973; Wainwright and Dillon, 1969; Preston and Preston, 1975; Murdock, 1978a, b), and eventually to complete overgrowth by encrusting organisms (Kinzie, 1970, 1974; Wahle, 1980; and references therein). The ultimate extent and duration of the various effects of injury are determined largely by the time required to regenerate the lost tissue and cover the internal, proteinaceous axis (Kinzie, 1970, 1974; Kitting, 1975; Lang da Silveira and van't Hof, 1977; for other taxa: Glynn, 1976; Bak *et al.*, 1977; Jackson, 1977; Jackson and Palumbi, 1979; Palumbi and Jackson, 1982). Consequently, any intrinsic or extrinsic variable(s) affecting rates of

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regeneration may indirectly but profoundly affect the survivorship, fecundity, and general ability of the colony to perform basic biological and ecological functions.

In this paper, I examine two sources of variation in the *in situ* ability of Jamaican arborescent gorgonians to regenerate injuries simulating those occurring routinely in nature (Woodley *et al.*, 1981). The first experiment considered the influence of colony physiology and energetics on the regeneration rates in the common plexaurid, *Plexaura homomalla*. Specifically, it tested the separate effects of colony size, colony reproductive phase, and location of injury on rates of regeneration of equal sized wounds placed on co-occurring colonies. The second experiment examined the relative regeneration rates of three common plexaurid species across their depth ranges. It contrasted regeneration rates of equivalent injuries among replicate colonies of *P. homomalla*, *Plexaurella dichotoma*, and *Eunicea mammosa* in three reef zones in and near Discovery Bay, Jamaica.

The two experiments differed in rationale, chronology, methods, and implication. Therefore, I first describe methods common to both, followed by separate treatments of specific methods, results, and discussion for each experiment.

MATERIALS AND METHODS

Sites

Regeneration experiments were conducted *in situ* in four reef zones in and near Discovery Bay, Jamaica during winter 1977 and summer 1978 (Fig. 1). The zones differed primarily in depth, exposure to waves, and gorgonian abundance (Kinzie, 1970, 1973; Woodley *et al.*, 1981). Many of the habitat characteristics described below, particularly the topography and structure of the benthic communities, were significantly altered by the passage of Hurricane Allen in August 1980 (Woodley *et al.*, 1981). Consequently, these descriptions apply to pre-storm conditions only.

The Mixed Zone (Fig. 1, site 1) is a shallow (7 m) hardground seaward of the reef crest containing an abundant and diverse gorgonian fauna (mean colony density of 14.6/m²; see Woodley *et al.*, 1981 for survey methods). The East Fore Reef Terrace (Fig. 1, site 2; henceforth called the Terrace) is a gently sloping plain at 15 m, characterized by thickets of *Acropora cervicornis*, scattered massive corals and sponges, and a diverse gorgonian assemblage (mean densities of 2.9 colonies/m²). The Rear Zone (Fig. 1, site 3) lies slightly west of the mouth of Discovery Bay and immediately leeward of the reef crest in depths ranging from 0.5 m to 1.5 m. Gorgonians were relatively rare, with mean colony densities of 0.3/m². The Shallow East Fore Reef (Fig. 1, site 4) lies southeast of the Terrace (site 2) and immediately east of the mouth of the bay. Although no quantitative surveys were conducted here, the site was similar to the Mixed Zone (site 1) in most respects relevant to this study.

Species

The three species chosen for these experiments span a range of polyp and colony morphologies characteristic of common, reef dwelling Caribbean plexaurids (Bayer, 1961; Kinzie, 1970). All occur as adult colonies in each zone and are frequently among the dominant members of gorgonian assemblages throughout the Caribbean and southwestern Atlantic (Bayer, 1961; Kinzie, 1970, 1973; Opresko, 1973).

Plexaura homomalla is perhaps the most studied of the Caribbean gorgonians (*e.g.* Cary, 1914, 1918; Kinzie, 1970, 1973; Bayer and Weinheimer, 1974, and papers therein; Wahle 1980). Its colonies are relatively large (roughly 1 m) with either planar or bushy branching patterns (Kinzie 1970, 1974). Colonies possess relatively thick

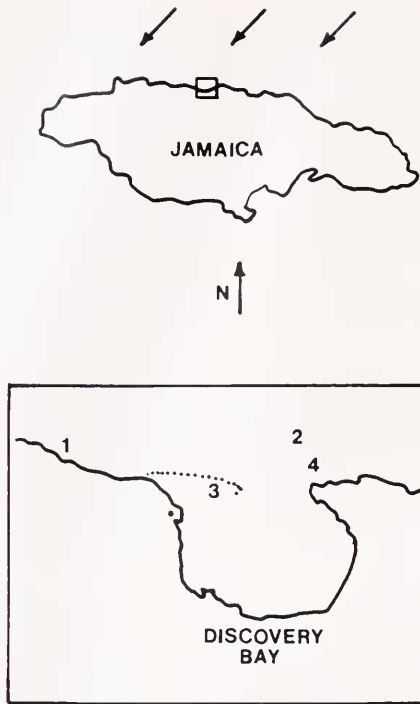


FIGURE 1. Location of experimental sites in four reef zones in and near Discovery Bay, Jamaica (inset): (1) Mixed Zone, (2) East Fore Reef Terrace, (3) Rear Zone, and (4) Shallow East Fore Reef. Dotted Line: reef crest; arrows: direction of prevailing winds and swells; asterix: D.B.M.L.

coenenchyme, and have small polyps with light spicular ornamentation on the verrucae (analogous to calyces among scleractinians; Bayer, 1961). *Plexaurella dichotoma* forms large (roughly 1.5 m), dichotomously branched colonies with thick coenenchyme, and long, unarmored polyps. *Eunicea mammosa* grows as relatively small (0.5 m), planar, candelabra-shaped colonies with thin coenenchyme and moderately long exert polyps which have heavily armored verrucae.

Techniques

Experimental injuries were placed on colonies *in situ* by carefully removing, with a scalpel, all tissue and sclerites (including the axial sheath) from around the internal, proteinaceous axis. The number, size, location, and timing of experimental injuries varied between the two experiments and are described separately below. Within each comparison of regeneration times, all injuries were equal in size (1.0 or 2.0 cm, measured by vernier calipers to within 0.1 mm) and were initiated simultaneously (within 48 hours of each other, unless otherwise specified).

The extent of tissue regrowth was recorded daily at 0700 hours. Regeneration was deemed complete when the internal axis was completely covered by gorgonian tissue and was no longer susceptible to fouling. The data, which do not satisfy the assumptions of analysis of variance (Sokal and Rohlf, 1969; Zar, 1974), were analyzed using non-parametric tests (*i.e.*, Kruskal-Wallis and Mann-Whitney).

RESULTS

Effects of colony physiology on regeneration in Plexaura homomalla

The following experiment examined the separate effects of colony size, colony reproductive phase, and injury location on regeneration rate among colonies of *Plexaura homomalla* on the Shallow East Fore Reef (Fig. 1, site 4). The experimental design (depicted schematically in Fig. 2) consisted of four paired comparisons of regeneration times (Fig. 2, bottom). A standard, simulated natural injury on 5 replicate control colonies (Fig. 2; labeled control) was compared to each of four other treatment groups differing from the controls in only one of the following variables: size, reproductive phase, or injury location (2 treatments). Controls consisted of 5 large (40–60 cm in height and width) replicate colonies, each with a single, one cm injury

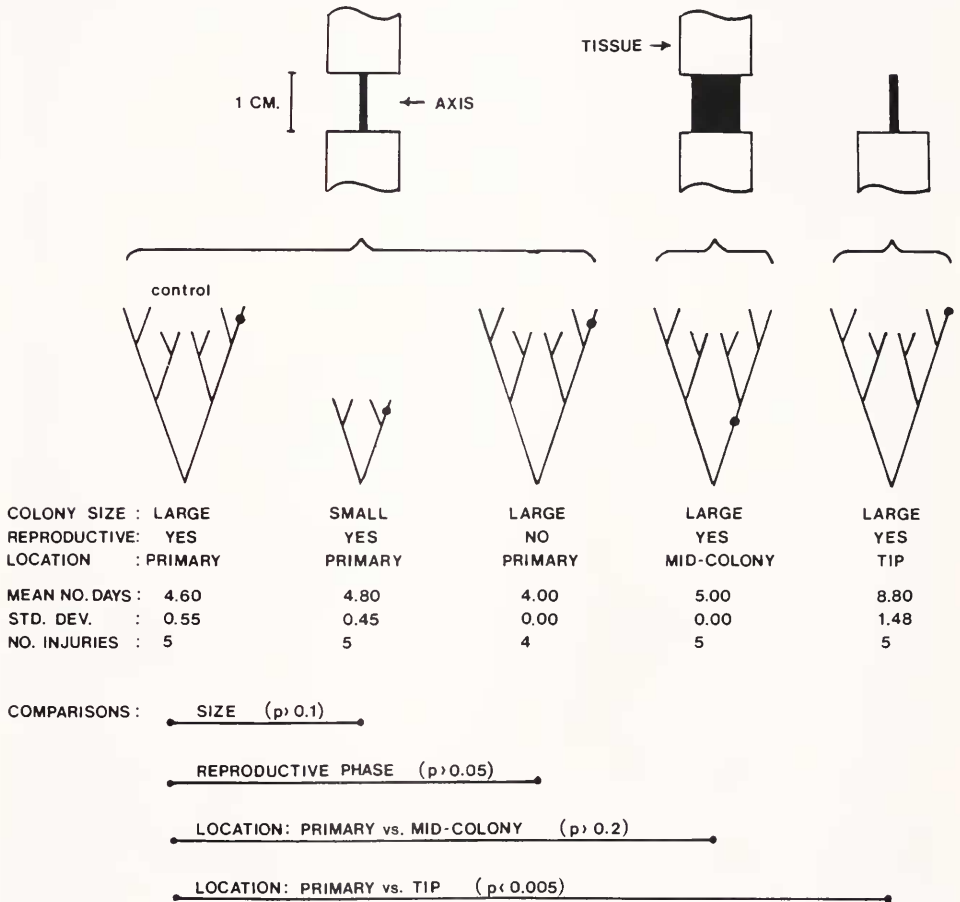


FIGURE 2. Colony physiology experiment: experimental design and results. Top: type of experimental injuries. Center: schematic of control and experimental colonies, each described below by three variables (size, reproductive phase, and injury location) and by results of regeneration experiments (mean number of days to regenerate, standard deviation, and total number of replicate injuries). Bottom: results of paired comparisons between controls and four treatment groups differing by the indicated variable (using Mann-Whitney tests).

placed mid-way down a terminal (primary) branch (Fig. 2, top and center, left). Methods and results for each of the four paired comparison are described below and in Figure 2.

With the exception of colonies in the non-reproductive treatment (described below), all experimental injuries were made in mid-July, 1978. Experimental colonies were equivalent in all obvious respects and were specifically chosen to have no external evidence of previous injury or other abnormalities. Consequently, this experiment controlled for many physiological and methodological variables potentially affecting regeneration rates within a species, including colony condition. I necessarily assumed that any other potential sources of variation affected all treatments equally or negligibly.

Colony size and regeneration. Connell (1973) and others (Fishelson 1973; Loya, 1976; Bak *et al.*, 1977) suggested that colony size might affect regeneration rates among scleractinians by limiting the availability of energy for regrowth within small colonies. Hence, assuming that energy is limiting to plexuarid gorgonians, one would predict slower regeneration rates (longer regeneration times) among small injured colonies differing from the larger controls only in colony size (10–20 cm *versus* 40–60 cm in height and width).

The results (paired comparison labeled Size, bottom of Fig. 2) showed that, while the trend in regeneration time was slightly in the predicted direction, small colonies did not regenerate significantly slower than large controls (4.80 *versus* 4.60 days; Mann-Whitney one-tailed test; $P > 0.1$). Thus, under these conditions, the presumed energetic differences between gorgonian colonies differing in size by up to 36-fold (calculated as height \times width) had no significant effect on their ability to regenerate lost tissue.

Colony reproductive phase and regeneration. It has been suggested for a variety of solitary and colonial taxa that, to the extent that energy is limiting, regeneration and sexual reproduction may compete for energy and thus may be mutually inhibitory. For example, repeated injury and regeneration may reduce subsequent sexual reproduction (bivalves: Trevaillon *et al.*, 1970; ectoprocts and sponges: Jackson, 1979; Jackson and Palumbi, 1979; zoanthids: Karlson, 1981, 1983). This experiment tested the converse hypotheses: that *P. homomalla* colonies at the peak of reproductive activity (controls) should regenerate slower than comparable but non-reproductive colonies not undergoing the simultaneous cost of gametogenesis. *P. homomalla* undergoes an annual reproductive cycle with gametogenesis peaking in late-June to mid-July (Goldberg and Hamilton, 1974; confirmed in Jamaica by *in situ* dissection and observation of gametes). Non-reproductive colonies used in this experiment were equivalent in all respects to the reproductive controls except that they were injured in December, 1977, when gametes were lacking or poorly developed (Goldberg and Hamilton 1974).

The results (paired comparison labeled Reproductive Phase in Fig. 2) show that, although the non-reproductive colonies followed the predicted trend of slightly faster regeneration rates (4.0 *versus* 4.60 days), the difference was not significant (Mann-Whitney one-tailed test; $P > 0.05$). Thus, under these conditions, the ability of *P. homomalla* to regenerate simulated, natural injuries was not significantly reduced by the presumed energetic costs of simultaneous gametogenesis.

Location of injury and regeneration. Natural injuries do not occur randomly within gorgonian colonies on northern Jamaican reefs. Rather, they tend to be concentrated on the colony periphery, and particularly on terminal or primary branches (Wahle, in prep.). This experiment compared the regeneration rates of injuries placed in three common locations on colonies of *P. homomalla*: primary branches (control), branch tips, and mid-colony (Fig. 2, top and center).

The results (Fig. 2, bottom) revealed no significant difference in regeneration rate between injuries in mid-colony and those on primary branches (5.00 *versus* 4.60 days; Mann-Whitney two-tailed test; $P > 0.2$). In contrast, injuries on branch tips regenerated significantly slower than those on primary branches of the controls (8.80 *versus* 4.60 days; Mann-Whitney one-tailed test, $P < 0.005$). Presumably, this two-fold difference in regeneration rate exists because injuries on branch tips have only one tissue front contributing to regrowth compared to two for injuries elsewhere in the colony (*sensu* Lang da Silveira and van't Hof, 1977, for *P. flexuosa*).

Among certain well-studied colonial taxa such as the ectoprocts, regenerative ability varies within colonies due to astogenetic gradients in zooid morphology and condition (Jackson and Palumbi, 1979; Palumbi and Jackson, 1982). That equivalent injuries (*i.e.*, mid-colony *versus* primary) did not vary in regeneration rate within these gorgonian colonies may reflect the apparent lack of comparable differentiation of function among polyps in the shallow water, Caribbean gorgonians (Bayer, 1961, 1973). Nevertheless, natural injuries to holdfasts and basal tissues often fail to regenerate (Cary, 1914, 1918; pers. obs. after Hurricane Allen, see Woodley *et al.*, 1981). This pattern, combined with the two-fold difference in regeneration rates between injuries on branch tips and those elsewhere on the colony, suggests that any systematic or predictable variation in the location of injury within colonies may seriously influence the ecological consequences of those injuries (particularly if on branch tips; Wahle in prep.).

Effects of species and reef zones on regeneration

Morphological and physiological differences among colonial taxa may be reflected in their ability to replace lost tissues (*e.g.*, for ectoprocts and sponges: Jackson and Palumbi, 1979). In addition, many plexaurid gorgonian species have relatively broad depth ranges across Caribbean reefs (Bayer, 1961; Kinzie 1970, 1973, 1974; Opresko, 1973). Consequently, conspecific colonies which are potentially within the same breeding population may experience very different environmental conditions, such as the availability of food or light (Kinzie, 1970) or the frequency of natural injury (Woodley *et al.*, 1981). Variation in these environmental conditions may in turn affect colony physiology, and specifically, rates of regeneration. This experiment examined regeneration rates among colonies of three common and morphologically distinct plexaurids living in three reef zones in and near Discovery Bay, Jamaica. Three related questions were addressed: 1) does a species' regenerative ability vary across its depth range; 2) do co-occurring species differ in regeneration rates within the same habitat; and 3) do the relative regeneration rates of the three species remain constant across their depth range, or are they differentially affected by changes in environmental conditions?

The species used in this experiment were *Plexaura homomalla*, *Plexaurella dichotoma*, and *Eunicea mammosa* (described in Methods). The experiments were conducted in the Mixed Zone, the East Fore Reef Terrace (Terrace), and the Rear Zone (Fig. 1, sites 1, 2, and 3 respectively), during late December, 1977. The experimental design consisted of placing two equivalent injuries on each of three replicate colonies for each of the three species in each of the three zones (Fig. 3; initial number of colonies = 27, number of injuries = 54). Final sample sizes, after loss of 2 replicate branches to storms and human disturbance, and elimination of 3 taxonomically ambiguous *Eunicea spp.* colonies, are given in Table I. Experimental injuries were made by completely removing 2 cm of tissue and sclerites mid-way down two terminal (primary) branches on each colony (Fig. 3). Paired injuries were placed on opposite

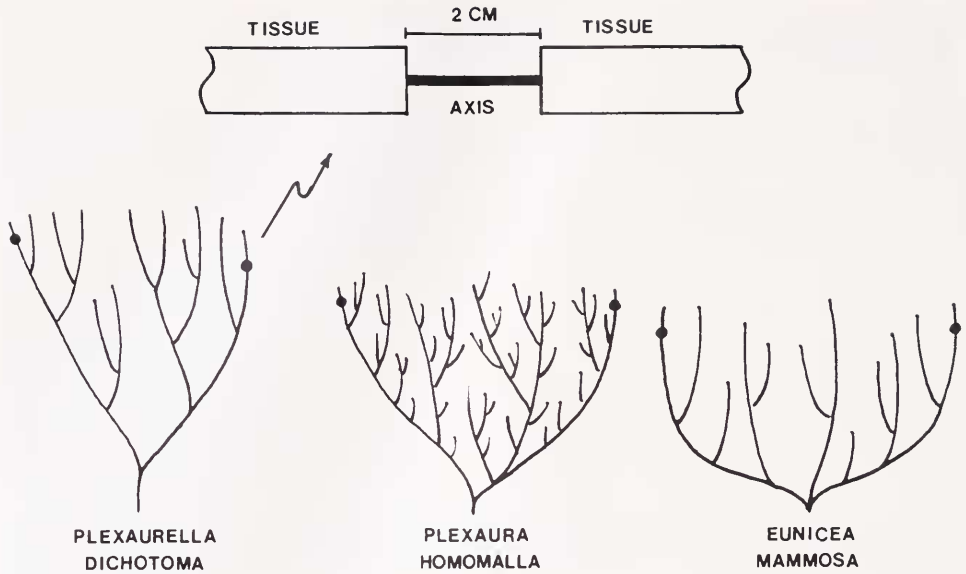


FIGURE 3. Species-Reef Zone experiment: experimental design showing type of injury (top), location of injuries on schematic representations of three species (center), and initial sample sizes (bottom).

sides of the colony to maximize their physiological independence and to minimize the potential for any influence of integration among regions of the colony (see Bayer, 1973; Murdock, 1978a, b). All experimental colonies were chosen for maximum size and minimum evidence of previous injury, and were thus presumed to be in optimal physiological condition within each zone.

TABLE I

Regeneration time (in days) of injuries on colonies of three species in three reef zones in and near Discovery Bay*

Species		Reef zones			Differences within species
		Mixed	Terr.	Rear	
<i>Plexaura homomalla</i>	\bar{x} :	(6.83)	(8.60)	(7.67)	$P < 0.05$
	s:	1.17	1.34	0.52	
	n:	6	5	6	
<i>Plexaurella dichotoma</i>	\bar{x} :	(6.67)	(9.00)	(10.60)	$P < 0.005$
	s:	0.52	1.55	0.89	
	n:	6	6	5	
<i>Eunicea mammosa</i>	\bar{x} :	(6.00)	(6.00)	(7.75)	$P > 0.05$
	s:	0.00	0.82	1.26	
	n:	4	4	4	
Differences within zones		$P > 0.1$	$P < 0.01$	$P < 0.01$	

* Values are: \bar{x} : mean regeneration time in days (parentheses); s: standard deviation; n: total number of injuries; P: significance levels for six Kruskal-Wallis tests of regeneration time within species or zones.

The effect of environment on specific regeneration rates. Within two of the three species examined (*Plexaura homomalla*, *Plexaurella dichotoma*), rates of regeneration differed significantly across the three reef zones (Table I; rows). The exception was seen among colonies of *Eunicea mammosa*, which showed no significant variation in regeneration rate across the reef (Kruskal-Wallis two-tailed test; $P > 0.05$). For each species (rows, Tables I and II) regeneration rates were generally fastest in the Mixed Zone, and slowest in the Rear Zone.

For each of the three reef zones, an overall, grand mean regeneration time was calculated for all co-occurring colonies, regardless of species. These three grand means were then ranked, with the zone having the fastest overall regeneration rate (least time) given primary rank (Table II, bottom row). These zone-specific regeneration ranks showed the same pattern as did the data for the individual species: increasing from Mixed to Rear Zone.

Differences in regeneration rate among co-occurring species. Within two of the three reef zones examined (Terrace and Rear Zone), regeneration rates differed significantly among the three co-occurring gorgonian species (Table I; columns). The exception was in the Mixed Zone, where regeneration rates of the three co-occurring species did not differ significantly (Kruskal-Wallis two-tailed test; $P > 0.1$). The relative regeneration rates (*i.e.*, fastest, intermediate, slowest) of the three species differed from zone to zone across the reef (Tables I and II, columns). In general however, the overall species ranking (Table II, right column) showed fastest rates of regeneration among colonies of *Eunicea mammosa*, followed by *Plexaura homomalla* and *Plexaurella dichotoma*.

DISCUSSION

Colony physiology and regeneration rates in P. homomalla

All organisms must allocate presumably limited energy to various biological functions such as growth, reproduction, regeneration and maintenance (*e.g.*, Charnov and Schaffer, 1973; Schaffer and Gadgil, 1975; Williams, 1975; Jackson, 1977; Stearns,

TABLE II

Mean regeneration rates of three species, ranked () for: conspecific colonies in different reef zones (rows); different species in the same zone (columns, parentheses); overall species rank (**); and overall zone rank (**)*

Species	Rank across	Reef zones			Overall species rank
		Mixed	Terr.	Rear	
<i>Plexaura homomalla</i>	zone:	1	3	2	2
	species:	(3)	(2)	(1)	
<i>Plexaurella dichotoma</i>	zone:	1	2	3	3
	species:	(2)	(3)	(3)	
<i>Eunicea mammosa</i>	zone:	1.5	1.5	3	1
	species:	(1)	(1)	(2)	
Overall zone rank		1	2	3	

* Ranks increase with decreasing mean regeneration rate (*i.e.*, 1, Fast; 3, slow).

** Overall ranks calculated as the ranked grand mean regeneration rate for each species across zones (right), and for each zone across species (bottom).

1977; Jackson and Palumbi, 1979; Karlson, 1981). The results of these experiments on regeneration among gorgonian colonies differing in some of the above variables (Fig. 2) suggest that energetic tradeoffs among competing biological functions may be more complex than previously thought for reef corals (Connell, 1973; Fishelson, 1973; Loya, 1976; Bak *et al.*, 1977).

For example, under the levels of injury tested in these experiments, rates of regeneration were independent of both colony size and reproductive phase (Fig. 2). These results, which contradict predictions based on simple energetic models, may have at least three possible and not necessarily mutually exclusive explanations. First, energy may seldom be limiting among reef-dwelling plexaurid gorgonians. This possibility will remain untestable until more is known about sources of nutrition and the energetic costs of growth, reproduction, and regeneration among these colonial animals. Second, the frequency and potential impact of injury on colony fitness may be sufficiently great to have selected for maintaining a permanent capacity to replace lost tissue, independent of other simultaneous energetic demands. Thus, for example, while the allocation of energy or other limited materials (*sensu* Lang da Silveira and van't Hof, 1977) may oscillate over time between growth and reproduction, gorgonians may possess a permanent and independent reserve available for future regeneration.

Third, this experiment measured rates of regeneration under normal, but relatively low levels of injury as compared to those occurring during catastrophic storms such as hurricanes (Woodley *et al.*, 1981). Moreover, experimental colonies were specifically chosen to have no evidence of previous injury or abnormalities which could potentially affect regenerative ability (*sensu* Lang da Silveira and van't Hof, 1977; Jackson and Palumbi, 1979; Palumbi and Jackson, 1982). Finally, the paired comparisons of regeneration rates consistently showed the predicted trends, but failed to differ significantly. Combined, these factors suggest that the effects on regeneration of colony size and reproductive phase (and perhaps of other aspects of colony energetics) may not become apparent until the intensity of injury (either natural or experimental) is considerably higher than that tested here. For example, gorgonians seem to be able to regenerate efficiently under low levels of natural injury (Kinzie, 1970; Birkeland and Gregory, 1975; Kitting, 1975, and references therein). However, repeated injury and regeneration among colonies of *Plexaura flexouosa* can inhibit future regeneration by depleting a critical population of rate-limiting, interstitial and transitional cells (Lang da Silveira and van't Hof, 1977). Thus, the predicted energetic constraints on regeneration may become important mainly among colonies with large, numerous, or repeated injuries. Such conditions could occur either routinely, in certain frequently disturbed reef zones, or during hurricanes (Cary, 1914, 1918; Woodley *et al.*, 1981).

Species, environment, and regeneration rates

Many common, Caribbean plexaurids extend in depth range across a variety of reef zones and environmental conditions (Bayer, 1961; Kinzie, 1970, 1973; Opresko, 1973). Among the three species examined, the influence of the environment on rates of regeneration was varied and complex (Tables I and II). Within two of the three species examined (*P. homomalla*, *P. dichotoma*), conspecific colonies differed significantly in regeneration rate across their depth range. In addition, within two of three reef zones examined (Terrace and Rear), co-occurring colonies of the three species differed significantly in regeneration rate. Moreover, the relative rankings of overall regeneration rates changed from zone to zone (Table II, across columns), and from species to species (Table II, among rows). This changing pattern suggests a potential interaction between species and environment on regeneration rate (hypothesis 3, above; Sokal and Rohlf, 1969).

Despite this degree of variation among species and reef zones, rates of regeneration were fastest and did not vary among co-occurring species in the Mixed Zone. This pattern suggests that the three species might have inherently similar regenerative capacities, but are differentially affected by changes in environment across their depth range. While the relation between environment and regeneration is undoubtedly complex, involving many variables, it may be influenced by frequencies of routine injury across the reef, and in the associated, cumulative energetic costs of repeated regeneration (*sensu* Lang da Silveira and van't Hof, 1977; Potts, 1977). For example, rates of regeneration (Tables I and II, bottom row) were fastest in the Mixed Zone, where previously surveyed natural injuries were relatively uncommon, and were slowest in the Rear Zone, where most gorgonian colonies were injured relatively heavily (Woodley *et al.*, 1981).

Injury and regeneration as ecological processes

The ability to regenerate lost tissue and skeleton is common to most of the marine invertebrate taxa which inhabit coral reefs (Mattson, 1976). Regeneration functions both as an integral part of the life history (Moment, 1951; Tardent, 1965), and as a response to injury (Wood-Jones, 1912; Cary, 1914, 1918; Kawaguti, 1937; Bayer, 1961; Mangum, 1964; Ebert, 1968; Kinzie, 1970, 1974; Trevaillon *et al.*, 1970; Connell, 1973; Fishelson, 1973; Birkeland and Gregory, 1975; Glynn, 1976; Loya, 1976; Bak *et al.*, 1977; Jackson, 1977, 1979; Lang da Silveira and van't Hof, 1977; Potts, 1977; Jackson and Palumbi, 1979; Hughes and Jackson, 1980; Karlson, 1981, 1983; Palumbi and Jackson, 1982; Hughes, 1983).

Despite its ubiquity however, the ecological role of regeneration remains relatively obscure, in part because neither injury nor regeneration immediately affect colony survivorship. Rather, their effects on colony fitness, and on the structure of sessile assemblages, may be subtle (and intimately related to colony physiology), delayed, and highly variable among different colonial taxa.

For example, regeneration of lost tissues often precludes the settlement of fouling organisms onto areas of exposed internal skeleton within the injured colony. Such fouling can have two important ecological consequences. First, settlement of competitive superiors can lead to the eventual overgrowth of the entire colony (Kinzie, 1970; Jackson and Palumbi, 1979; Palumbi and Jackson, 1982; and references therein). This potential relationship between injury, regeneration, survivorship, and abundance may have influenced patterns of gorgonian abundance in the three Jamaican reef zones examined here. Gorgonians were most common in the Mixed Zone (14.6 colonies/m²), where frequencies of natural injury were low (Woodley *et al.*, 1981) and rates of regeneration were fast (Tables I and II). Conversely, gorgonian abundances were low (0.3 colonies/m²) in the Rear Zone, where frequencies of injury were high (Woodley *et al.*, 1981) and rates of regeneration were slow (Tables I and II). Clearly however, these patterns are probably affected by many other variables as well.

The second consequence of fouling is the immediate addition of new organisms to benthic assemblages. By preventing recruitment of other organisms onto surviving colonies, regeneration may profoundly influence the structure and composition of benthic communities (Bak *et al.*, 1977; Jackson and Palumbi, 1979; Palumbi and Jackson, 1982). The impact of such fouling, however, will vary with the size, growth form, and competitive ability of the fouling taxa in relation to that of the injured colony. For example, recruitment of encrusting organisms (*e.g.*, bryozoans, foraminiferans, and crustose algae) onto similar taxa living in the relatively two-dimensional, cryptic community (Jackson, 1979) may have much greater effects on community

structure (Jackson and Palumbi, 1979; Palumbi and Jackson, 1982) than would fouling by comparable organisms onto the larger colonial animals of the open reef. Although all injuries in these experiments were fouled by various encrusting taxa (filamentous algae, athecate hydroids; with varying effects on regeneration rate) all gorgonian colonies were able to fully regenerate over these fouling organisms (see also Bak *et al.*, 1977).

Thus, among reef communities differing in scale (*e.g.*, cryptic *versus* open reef; Jackson, 1979), similar processes of injury, regeneration, and fouling may have very different ecological consequences. In the cryptic community, the major ecological effect of injury may be its influence on recruitment of comparable organisms into the community (Jackson and Palumbi, 1979; Palumbi and Jackson, 1982). On the open reef, where many fouling taxa are small relative to injured gorgonians, corals, or sponges, the primary influence of injury and regeneration may be more on colony physiology than on colony numbers. For example, in many gorgonian species, both behavior and reproduction are integrated and synchronized among most polyps within the colony (behavior: Wainwright and Dillon, 1969; Bayer, 1973; Preston and Preston, 1975; reproduction: Bayer, 1973, 1974; Goldberg and Hamiton, 1974). Injuries have the potential to temporarily or permanently disrupt these and other aspects of a colony-wide physiological integration by isolating distal regions of the colony from the main body of polyps (Wahle, 1983). Thus, a major role of regeneration among reef dwelling gorgonians, and among other open reef colonial taxa, may be to restore colony-wide integration of critical biological and ecological functions disrupted by injury.

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